Environmental and Regional Determinants of *Anopheles* (Diptera: Culicidae) Larval Distribution in Belize, Central America

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ABSTRACT Surveys of *Anopheles* larval habitats in northern Belize were carried out during September 1990 and April 1991. At each site, larvae were collected and the physical and chemical characteristics of water and species composition of aquatic vegetation were measured or estimated. Data on presence or absence of four species, *Anopheles albimanus* Wiedemann, *A. crucians* Wiedemann, *A. pseudopunctipennis* Theobald, and *A. argyritarsis* Robineau-Desvoidy, were used for analysis of associations with environmental factors, habitat types, and regions. Using significantly contributing environmental variables, discriminant functions (DF) were constructed for the *Anopheles* species, except for *A. argyritarsis* whose distribution could be predicted solely by altitude. The stability of DFs was checked by cross-validation runs. The DF for *A. pseudopunctipennis* was 93% accurate in predicting positive habitats. Predictions based on DFs for *A. albimanus* and *A. crucians* were 74 and 80% accurate, respectively. Of the four *Anopheles* species present in the study area, *A. albimanus* was the most common. Together with *A. crucians*, it occurred mostly on the coastal plain, and both species were present in both wet and dry seasons. *Anopheles albimanus* was positively associated with cyanobacterial mats and submersed–periphyton habitat types and negatively associated with the filamentous algae habitat type. *A. crucians* was positively associated with *Eleocharis*–periphyton habitat type. *A. pseudopunctipennis* and *A. argyritarsis* were common only during the dry season and their distribution was limited to the Karst and Mountain Pine Ridge regions. Both species were positively associated with the filamentous algae habitat type, and *A. argyritarsis* was also positively associated with the rock pools habitat type. Physical factors (e.g., water depth, water temperature, and oxygen content) were usually marginally correlated with larval occurrence. Dominant plant growth forms, such as filamentous algae, cyanobacterial mats, and submersed macrophytes showed the closest association with the larvae of particular *Anopheles* species. Our results demonstrated the controlling influence of dominant aquatic vegetation on larval presence.

KEY WORDS larval habitats, aquatic vegetation, *Anopheles* spp.

GEOMORPHOLOGY affects the hydrology of a region; i.e., distribution and seasonal dynamics of lakes, rivers, streams, and pools. Water quality in these different water bodies is influenced by rock and soil chemistry, vegetation of the surrounding landscape, and human activities. Both hydrology and water chemistry determine the type of aquatic vegetation present in lakes, pools, and streams. Shallow, quiet water with aquatic vegetation seems optimal for oviposition and larval development of most mosquito species. Descriptions of requirements of individual species for specific characteristics of larval habitats have generally been rather vague. A few attempts to describe the relationships between larvae and different environmental factors can be found in papers by Rioux et al. (1968), Hagstrum & Gunstream (1971), Hall (1972), Vrtiska & Pappas (1984), Gabinaud (1987), Orr & Resh (1989), Savage et al. (1990), and Rejmankova et al. (1991).

Obviously, if we can point out individual environmental factors related to the presence of larvae, then groups of individual factors are probably characteristic of specific larval habitats, which, in turn, might be related to distinct geo-

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graphic regions. Once the connections are made between the fine scale of individual larval habitats and a coarse scale of their regional distribution, our understanding of mosquito larval ecology, specifically with regard to malaria transmission, will be greatly improved.

The country of Belize, located south of the Yucatan Peninsula on the Atlantic coast of Central America (Fig. 1), provides a great variety of ecological settings as foci of malaria transmission. Komp (1941) first reported the occurrence of *Anopheles darlingi* Root in Belize. This finding was verified by Kumm & Ram (1941), who also documented the occurrence of malaria-infected specimens of *A. darlingi* and *A. vestitipennis* Dyar & Knab. Additionally, Kumm & Ram (1941) reported the presence of seven other species of *Anopheles;* i.e., *A. albimanus* Wiedemann, *A. pseudopunctipennis* Theobald, *A. punctimacula* Dyar & Knab, *A. apicimacula* Dyar & Knab, *A. eiseni* Coquillett, *A. argyritarsis* Robineau-Desvoidy, and *A. crucians* Wiedemann. Bertram (1971) reported collecting all of these species, except *A. darlingi,* in Belize. Bertram's work, which emphasized the ecology of adult mosquitoes, is practically the only source of information on the spatial and seasonal distribution of anophelines in Belize.

Not only in Belize but throughout Central America, larval ecology of malaria vectors has been the subject of infrequent and sporadic studies. Review papers by Rozeboom (1941), Watson & Hewitt (1941), and Bates (1949) described the seasonal and spatial distribution of *A. albimanus* and *A. pseudopunctipennis*. Breeland (1972) presented specific information on the seasonal and spatial distribution of these vectors along the Pacific coast of El Salvador. Bailey et al. (1981) studied the distribution of *A. albimanus* larvae in estuarine habitats of El Salvador. The relationships of *A. albimanus* and *A. pseudopunctipennis* larvae to dominant aquatic plants and environmental factors in southern Chiapas, Mexico, have been reported by Savage et al. (1990) and Rejmankova et al. (1991). A hierarchical method for classifying larval habitats into habitat types was subsequently suggested by Rejmankova et al. (1992).

In addition to *A. albimanus* and *A. pseudopunctipennis,* several other *Anopheles* occur in Central America. Recently, *A. vestitipennis,* previously considered to be a relatively unimportant malaria vector, was found to transmit malaria in areas within Mexico and Guatemala (Loyola et al. 1991, Padilla et al. 1992). Roberts et al. (1993) found this species to be of potential importance as a vector of malaria in Belize. These recent findings are indicators of our poor understanding of vectorial roles of *Anopheles* in much of Central America. Malaria rates in Belize are increasing, so the issues of species distributions and vectorial roles are increasingly important to the health and welfare of the Belizean population.

An array of vegetation types exists in Belize. Most of the primary tropical deciduous forests have been disturbed by intensive logging for mahogany and logwood and traditional slash-and-burn agriculture. Extensive areas on the coastal plain are covered with seasonally inundated savanna, lowland pine forest, and freshwater swamp forest. Mangrove swamps are common along the coast and extend inland wherever brackish water occurs. Sugarcane, grown mostly in northern Belize, is a prime agricultural crop. Citrus-growing is becoming more important, with large areas of forest in the Cayo and Stann Creek districts currently being cleared for citrus cultivation.

In September 1990, we initiated a surveillance program to obtain population-based data on the malaria vectors in Belize. The quantity of environmental data compiled was greater than normally collected in field surveys. This allowed the larval–environmental associations to be studied from different levels of detail, ranging from the individual habitat to a regional level. The most detailed analysis was performed at the individual habitat level, using environmental variables that might affect oviposition as well as larval distribution, density, development, and survival. A second approach was based on a more holistic view of larval habitats. Using this approach, habitats were described according to their dominant vegetation, classified into habitat types, then examined for association between habitat types and the presence or absence of *Anopheles* species. The third approach to data analysis involved assessment of associations at the regional level.

Program objectives were to document which vector species were present in northern Belize, to define the habitat ranges of these species, and to determine whether their presence or absence could be predicted by environmental factors, habitat types, or regional characteristics. Reported herein are the results of habitat analysis and regional distribution of *A. albimanus, A. pseudopunctipennis, A. crucians,* and *A. argyritarsis*.

Materials and Methods

Study Area. With an area of 23,000 km^2 and a population of ≈180,000, Belize is a country with the lowest population density in Central America. Lowlands of Belize are characterized by a variety of wetlands, freshwater and brackish, seasonal and permanent. Montane and foothill regions include many streams and rivers. The hydrological and vegetational diversity results in a wide variety of mosquito larval habitats.

The amount of rainfall increases from ≈1,300 mm annually in the north to 2,400 mm around Belize City. The normal dry season is from January through April and is shorter and less severe

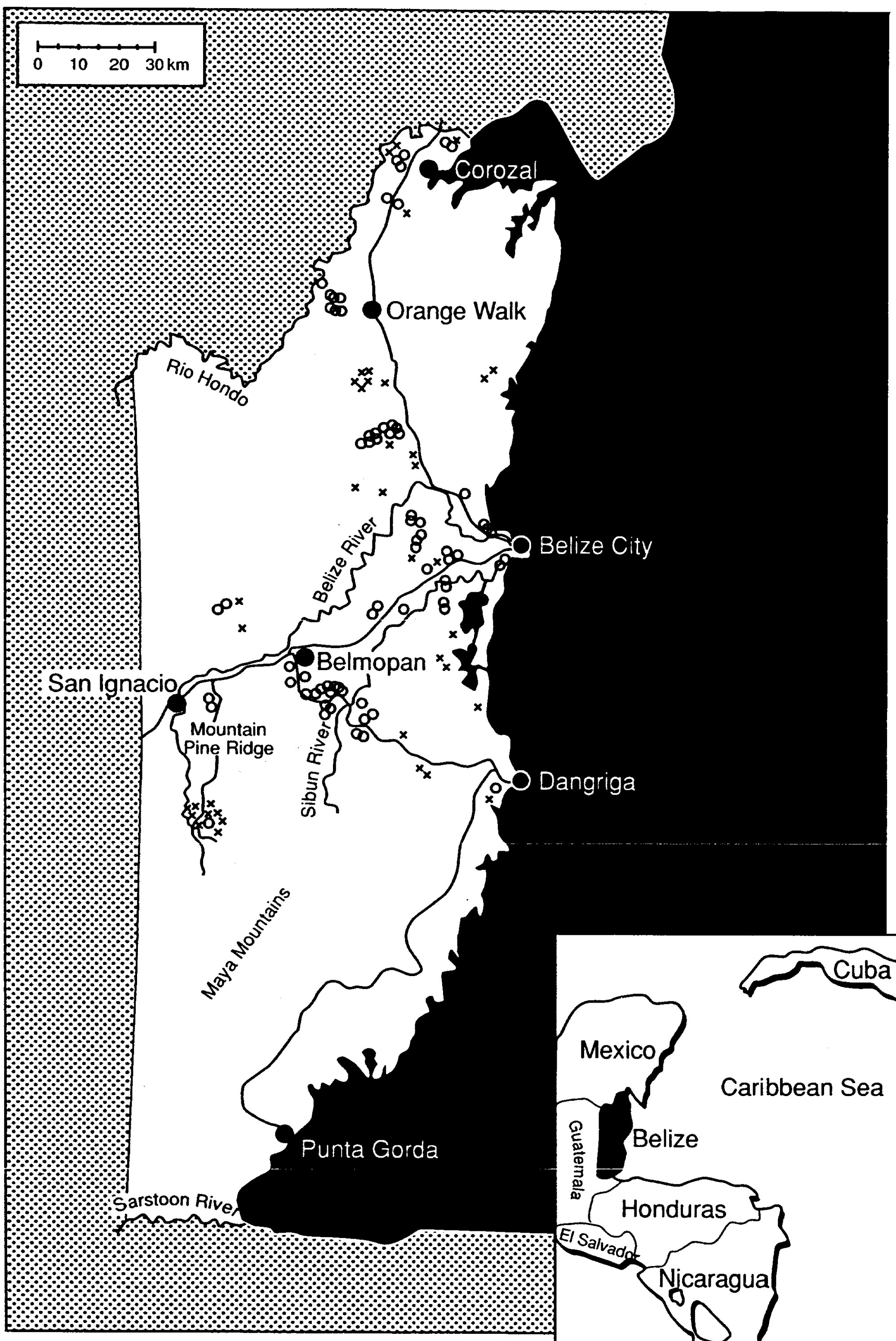

Fig. 1. Map of Belize with location of sampling sites in the wet (September 1990) and dry (April 1991) seasons. Circles indicate sites visited during both seasons. Crosses indicate sites added in the dry season.

than at comparable latitudes on the Pacific coast of Central America.

Our survey sites were distributed in the northern part of Belize from Dangriga north, covering Corozal, Belize, Orange Walk, and parts of Cayo and Stann Creek districts (Fig. 1). This northern area includes three distinct physiographic regions: flat coastal and inland plain (CP), karst and foothills (KARST), and Mountain Pine Ridge (MPR), which all differ in their topography, geology, hydrology, soils and, consequently, vegetation cover (Hartshorn et al. 1984). The terms "regional" and "region" are used in this article for physiographic regions of northern Belize on a scale of 10^2–10^3 km^2.

The MPR region includes fast-flowing rivers and streams with nutrient-poor waters of very low mineral content. No extensive wetlands occur in this region; therefore, mosquito habitats exist in the form of river pools with filamentous algae and occasional graminoids. In the KARST region, larval habitats are also mostly associated with rivers. These rivers are slower than in the MPR and their waters are richer in minerals, specifically calcium. Pasture ponds and small lagoons with different types of aquatic vegetation are also present in this region. The CP includes both fresh and brackish waters and provides very diverse and often extensive habitats ranging from almost monospecific marshes dominated by a sedge, *Eleocharis interstincta* (nomenclature for vascular plants follows Standley & Steyermark 1946–1977), to species-rich ponds and lagoons.

Larval Sampling. Surveys of a wide range of mosquito larval habitats were conducted in the northern part of Belize in both the wet (September 1990) and dry (April 1991) seasons. A mosquito larval habitat is defined as a body of water with uniform vegetation and a specific water chemistry (Rejmankova et al. 1992). In the wet season, larval habitats were sampled at 75 different sites (see Fig. 1). In the dry season, the 75 sites previously surveyed in the wet season were visited and some new sites were added because many of the wet-season locations were dry. The total number of sites with water in the dry season including both the old and added sites was 73.

The following data were recorded for each habitat: total percentage of emergent, floating, or submersed vegetation, algal mats, and detritus; percentage of cover of individual plant species; amount of phytoplankton (measured fluorometrically as chlorophyll *a* concentration); water conductivity; pH; and dissolved oxygen. Water analyses were conducted for total suspended solids, particulate organic matter, nitrate and ammonia nitrogen (NO_3, NH_4), orthophosphate phosphorus (PO_4), and major cations (Na, K, Ca, Mg) using standard limnological methods (APHA 1985). Thirty dips for mosquito larvae were taken from each habitat. Although a greater number of dips was not practically feasible, we already knew from earlier work that 30 dips provided a rough estimate of population density (Savage et al. 1990; Rejmankova et al. 1991). To process the samples, larvae and pupae were transported to the laboratory in Belize City and reared to obtain adults with associated immature exuviae for identification, study, and future reference. Some fourth instars were also preserved from most collections.

Larval Occurrence and Environmental Factors. Data on the occurrences of larvae of different *Anopheles* species were related to environmental factors. Because of large variations in larval density, most analyses were conducted using information on the presence–absence of individual species. The environmental variables were subjected to either log transformation (conductivity) or the angular transformation (all plant variables were expressed as percentage values) before further analysis. The two-tailed *t* test was used to compare the group means of environmental variables for sites with or without larvae.

Discriminant Analysis. Relationships between the presence–absence of each *Anopheles* species in the dry season data set and the selected environmental variables were further explored using discriminant analysis (Tabachnick & Fidell 1989). Our goal was to select a reduced set of variables for predicting the distribution of each species. The discriminant functions were first calculated using all the environmental variables identified by *t* test as having significantly different group means for sites with and without larvae. Subsequently, the variables that did not contribute significantly to the respective discriminant functions were deleted. The final number of variables used was four for *A. albimanus* and *A. crucians* and three for *A. pseudopunctipennis*. We did not calculate the discriminant function for *A. argyritarsis*, whose distribution could be predicted solely by altitude.

To assess the predictive power of the respective discriminant functions, five randomly selected subsets of data were used to calculate the functions that were subsequently applied to independent data subsets (cross-validation technique; see Tabachnick & Fidell 1989).

Habitat Types. Because of substantial habitat diversity, the individual habitats, defined by dominant plant species, were categorized into higher units, subsequently referred to as habitat types (Rejmankova et al. 1992). Cluster analysis (Orloci 1978) based on the absolute distance dissimilarity after the angular transformation of the environmental variables (plant cover) was used for delineation of nine habitat types based on the wet-season data. During dry-season sampling, a site was ascribed to a habitat type before sampling for larvae was done. Three additional distinctive habitat types were sampled in the dry season: rock pools without filamentous algae, detritus, and planktonic algae. Based on the aver-

Table 1. Average specific conductivity ± SD for sampling sites in the four regions in the wet and dry seasons

Season	Mountain pine ridge	Karst	Coastal plain	
			Fresh	Brackish
Wet	14	144 ± 129	91 ± 71	2,186 ± 820
Dry	42 ± 12	198 ± 216	183 ± 97	1,826 ± 891

age number of larvae per dip, the habitat types were ranked as high (>1), medium (0.1–1), and low (<0.1).

Larval Distribution Within Defined Habitat Types and Geographic Regions. *G* tests of independence (Zar 1984) were calculated to determine the associations between the presence–absence of each vector species and habitat types and regions, respectively.

Results

Dry-season sampling revealed that 66% of wet-season habitats were dry during the dry season, 7% were significantly smaller, and 27% were relatively unchanged. Water conductivity was significantly higher in the dry season in habitats in both MPR and CP (fresh), whereas it did not differ much in KARST and CP (brackish) (Table 1). Plant diversity was much higher in the wet season than in the dry season (see list of plant species in Appendix 1), mainly because species-rich edges of ponds and lagoons that were flooded during the wet season dried up and ceased being larval habitats during the dry season.

Larval Occurrence and Environmental Factors. Physical factors (e.g., water depth, water temperature, oxygen content) were usually marginally correlated with larval occurrence. Dominant plant growth forms such as filamentous algae, cyanobacterial mats, and submersed macrophytes showed the closest association with the larvae of particular *Anopheles* species.

Discriminant Analysis. Using the environmental variables with significantly different group means for sites with larvae present versus absent (Tables 2 and 3), we calculated discriminant functions for the dry season for all the *Anopheles* species (Fig. 2 a–c), except for *A. argyritarsis*.

For *A. albimanus*, 10 environmental variables were significantly different for dry-season sites with and without larvae (Table 2). Of these variables, only cover percentage of submersed plants, cover percentage of cyanobacterial mats, altitude, and temperature contributed significantly to the discriminant function by 44, 30, 14, and 12%, respectively. The discriminant function for the whole data set correctly predicted the presence of larvae in 74% of all sites and correctly predicted the absence of larvae in 91% of the sites (Fig. 2a; Table 4). Five randomly selected subsets of data were then used to construct the discriminant functions. When these functions were tested on the remaining independent subsets of data, the correctly predicted percentage of sites with larvae varied from 45 to 89%. Additionally, 81–95% of sites without larvae were correctly classified (Table 4). Cover percentage of periphyton, detritus, and emergent plants and habitat area were used as variables for constructing discriminant functions for *A. crucians* (Fig. 2b; Table 5) contributing by 44, 24, 22, and 10%, respectively, to the predictive power of the DF. Using the entire data set, the function correctly classified 80% of sites for the presence of larvae and 94% for the absence of larvae. Using five randomly selected subsets, correct predictions varied from 33 to 100% and from 84 to 91% for presence and absence of larvae, respectively. Cover percentage of filamentous algae, altitude, and water depth were used to construct the discriminant function for *A. pseudopunctipennis* (Fig. 2c; Table 6) contributing 81, 11, and 8%, respectively, to the predictive power of the DF. With the entire data set, the function correctly classified 93% of the sites for presence of larvae and 93% for absence of larvae. For the five randomly selected subsets, correct predictions ranged from 78 to 100% for positive sites and from 87 to 100% for negative sites.

Habitat Types. During the wet and dry season collections, nine and 12 major habitat-types were distinguished respectively, as defined by a dominant plant species, genera or life form (Fig. 3; Table 7). Of these twelve habitat types, five represented emergent macrophytes (including mangroves), two belonged to floating hydrophytes, and three were characterized by submersed hydrophytes. Three remaining habitat types (rock pools with no filamentous algae, detritus, and planktonic algae) did not contain any macrophytic vegetation. The detailed description of habitat types is given in Appendix 2. As shown in Table 7, habitat types cyanobacterial mats, submersed macrophytes–periphyton, *Nymphaea–Limnanthemum*, and mangroves were relatively stable with three of five, two of five, three of seven, and two of five sites staying the same in both the wet and dry seasons, respectively. Most sites sampled during the wet season that belonged to graminoids and *Eleocharis interstincta*–periphyton habitat types and all sites of *Typha–Cladium* habitat type were dry during the dry season. Three sites of wet-season graminoids habitat type, two sites of cyanobacterial mats habitat type, and one site each of *Eleocharis interstincta*–periphyton and *Nymphaea–Limnanthemum* habitat types developed into different habitat types during the transition from wet to dry seasons.

Larval Distribution Among Habitat Types. The tendency of water bodies to contain the same habitat type in both seasons (16 of 25) and, consequently, to support larvae of the same spe-

Table 2. Comparison of significantly different group means (±SD) of environmental variables measured in the dry season (two-tailed *t* test)

Environmental variable	Larvae Present	Larvae Absent	$P <$ [a]
	Anopheles albimanus		
No. sites	27	46	—
% Cyanobacterial mats	20.4 (31.5)	1.8 (10.3)	0.0001*
% Submersed	29.0 (38.1)	2.1 (11.7)	0.0001*
% Filamentous algae	3.3 (17.3)	17.4 (28.0)	0.005*
Habitat area, m^2	25.6 (41.3)	7.5 (11.2)	0.006
Water body area, m^2	1,848.8 (2,600.0)	644.8 (1,200.0)	0.009
% Periphyton	5.8 (16.1)	0.6 (1.5)	0.01*
Altitude, m	35.3 (56.9)	118.3 (171.8)	0.02
Conductivity µmhos/m	1,086.5 (1,087.0)	738.9 (1,610.6)	0.03+
Temperature, °C	32.8 (2.1)	31.6 (1.9)	0.03
Oxygen, ppm	8.6 (3.7)	7.1 (2.6)	0.058
	Anopheles crucians		
No. sites	10	63	—
% Periphyton	12.9 (25.3)	0.9 (2.2)	0.0001*
% Emersed	28.2 (28.9)	11.4 (23.0)	0.01*
% Detritus	12.0 (28.2)	1.9 (9.7)	0.02*
Habitat area, m^2	30.0 (60.2)	11.6 (18.0)	0.05
	Anopheles pseudopunctipennis		
No. sites	14	59	—
% Filamentous algae	48.9 (31.1)	3.5 (13.5)	0.0001*
Conductivity, µmhos/m	102.0 (94.6)	1,049.1 (1,549.5)	0.0002+
Water depth, cm	8.0 (9.45)	24.0 (15.5)	0.0004
Altitude, m	192.1 (178.0)	62.7 (126.4)	0.002
% Emersed	0.07 (0.26)	17.0 (26.1)	0.004*
Temperature, °C	30.9 (2.5)	32.3 (1.9)	0.02
Water body area, m^2	1.8 (2.6)	1,348.0 (2,054.0)	0.02
% Submersed	0.0 (0.0)	14.9 (30.4)	0.03*
Habitat area, m^2	1.4 (1.5)	17.1 (30.1)	0.05
	Anopheles argyritarsis		
No. sites	9	64	—
Altitude, m	453.0 (40.0)	36.0 (47.5)	0.0001
Conductivity, µmhos/m	42.2 (12.7)	983.5 (1,504.2)	0.0001+
Temperature, °C	33.9 (1.6)	31.8 (2.0)	0.005
% Emersed	0.11 (0.33)	15.6 (25.5)	0.03*
Water body area, m^2	0.8 (0.8)	1,243.3 (2,004.6)	0.058

[a] *, after angular transformation; +, after log transformation.

Table 3. Comparison of significantly different group means (±SD) of environmental variables measured in the wet season (two-tailed *t* test)

Environmental variable[a]	Larvae		$P <$ [b]
	Present	Absent	
	Anopheles albimanus		
No. sites	18	57	—
% Cyanobacterial mats	24.4 (24.5)	3.51 (7.26)	0.0001*
POM, ppm	53.26 (94.84)	3.55 (4.19)	0.0001
Ca^{++}, ppm	168.41 (206.26)	52.67 (80.75)	0.0009
TSS, ppm	69.92 (121.27)	9.77 (11.16)	0.0004
Mg^{++}, ppm	54.65 (67.25)	16.91 (31.85)	0.002
% Detritus	8.16 (16.05)	1.28 (4.34)	0.003*
pH	7.57 (0.63)	7.10 (0.80)	0.03
	Anopheles crucians		
No. sites	9	66	—
pH	6.63 (0.76)	7.30 (0.76)	0.02

[a] POM, particulate organic matter; TSS, total suspended solids.
[b] *, after angular transformation; +, after log transformation.

cies, was significant (G test; $P < 0.025$). Larval density was much higher in the dry season than in the wet season (Fig. 3). All four *Anopheles* species were present in the dry season, whereas only *A. albimanus* and *A. crucians* were found in the wet season. In the dry season, cyanobacterial mats, filamentous algae, and submersed–periphyton represented high larval density habitat types (>1 larva per dip); *Eleocharis*–periphyton, broadleaved, rock pools, detritus, and planktonic algae belonged to medium-density habitat types (0.1–1 larva per dip); and the rest were low-density habitat types (<0.1 larva per dip). In the wet season, high densities of larvae were found in cyanobacterial mats and filamentous algae habitat types, the graminoids habitat type produced medium numbers of larvae, and the remaining habitat types produced very few larvae. Because of a large variability in larval counts and a low number of replicates, we did not find statistically significant differences in larval density between habitat types (Sheffe multiple comparison test), except for a wet-season difference between cyanobacterial mats and all remaining habitat-types.

The results of the G test of independence between habitat types and *Anopheles* species (Fig. 4) show a highly significant positive association between *A. albimanus* and the cyanobacterial mats and submersed–periphyton habitat types, and a highly significant negative association between *A. albimanus* and filamentous algae habitat type. *A. crucians* was positively associated with the *Eleocharis*–periphyton habitat type and slightly negatively associated with the filamentous algae habitat type. *A. pseudopunctipennis* and *A. argyritarsis* were positively associated with the filamentous algae habitat type, and *A. argyritarsis* was positively associated with the rock pools (no algae) habitat type.

Regional Distribution. Fig. 5 summarizes the data on distribution of *Anopheles* species among the different regions of the study area. *A. argyritarsis* was found only in rock pools of MPR. The rock pools are characterized by low water conductivity with very low content of minerals. *A. pseudopunctipennis* occurred in both MPR and KARST, always in river pools with filamentous algae. Water in the KARST region has a higher content of minerals, specifically calcium (>20 ppm). *A. crucians* was found mainly in habitats associated with CP (fresh) (water conductivity comparable to KARST), even though it was occasionally present in KARST and CP (brackish) as well. The highest larval densities of *A. albimanus* were found in habitats of CP (brackish), but this species was quite common in KARST and CP (fresh) as well. Statistical significance of these associations is expressed in Fig. 6.

Discussion

Discriminant Functions. The discriminant functions for presence of *A. albimanus* and *A. pseudopunctipennis* using data from southern Chiapas, Mexico, were published by Savage et al. (1990). The authors used slightly different techniques to construct their DF and select the significant variables. Yet the final selection of important variables for *A. pseudopunctipennis* was the same as in this paper; i.e., filamentous algae, altitude, and water depth. Consequently,

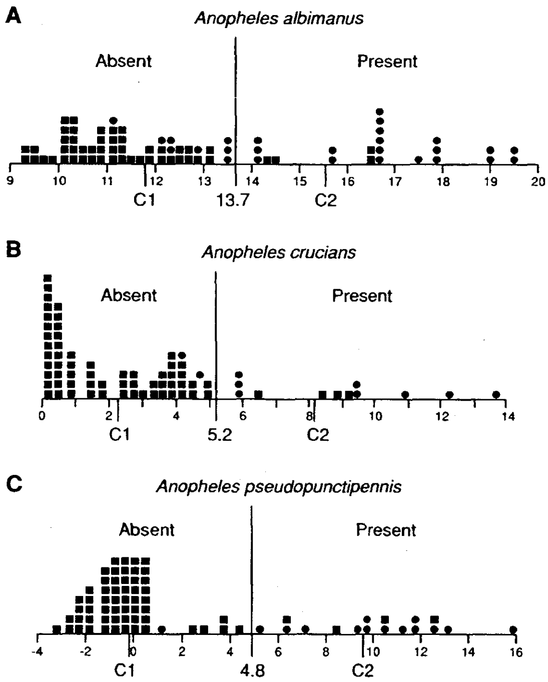

Fig. 2. (A) Discriminant function (Z, see Table 4) for *A. albimanus.* ■, Species absent; ○, species present. C1 and C2, Group centroids. (B) Discriminant function (Z, see Table 5) for *A. crucians.* ■, Species absent; ○, species present. C1 and C2, Group centroids. (C) Discriminant function (Z, see Table 6) for *A. pseudopunctipennis.* ■, Species absent; ○, species present. C1 and C2, Group centroids.

we are quite confident that the DF for *A. pseudopunctipennis* is broadly applicable to other northern areas of Central America. The environmental variables used, especially the cover percentage of filamentous algae that contributes ≈80% to the predictive power of the DF, appear to exert a controlling influence on the distribution of this species.

Predictions based on the DF for *A. albimanus* were less accurate than those for *A. pseudopunctipennis*. The DF for *A. albimanus* could not be compared with that of Savage et al. (1990) because their function included the cover of *Eichhornia*, a floating aquatic macrophyte, as one variable; *Eichhornia* was not found in Belize. The variables selected for DF were, in descending order of importance, submersed macrophytes, cyanobacterial mats, altitude, and water temperature. When the DF derived from the dry-season data was applied to the wet-season data set, it resulted in 72% of correctly predicted positive sites and 49% of correctly predicted sites with larvae absent. This is (at least for the positive sites) in the range of predictive values found for *A. albimanus*. The lower predictive value of *A. albimanus* DFs compared with DFs for *A. pseudopunctipennis* may be caused by the broader range of environmental conditions under which *A. albimanus* larvae occur. Variables associated with the presence of *A. albimanus* larvae in habitats in Belize were quite different from those in Mexico. In Mexico, the main variables were phytoplankton (unicellular green algae) in both seasons and *Eichhornia* in the dry season and Cyperaceae and phosphates in the wet season. None of these variables was linked with the distribution of *A. albimanus* larvae in Belize. Few habitats supported measurable quantities of phytoplankton in Belize, whereas many habitats were rich in phytoplankton in Mexico. This may be because waters in southern Chiapas contained generally 2–3 times higher concentrations of major nutrients (nitrogen, phosphorus) because of the volcanic origin of nutrient-rich soils in the area, abundant cattle manure, and extensive use of fertilizers. In the limestone regions of Belize, waters were poor in nitrogen and phosphorus but rich in calcium, both conditions being rather unfavorable for the growth of phytoplankton. On the other hand, extensive benthic cyanobacterial mats capable of nitrogen fixation, and submersed macrophytes overgrown with periphyton, were quite common in Belize, but they were not encountered in habitats in Mexico. Stands of several Cyperaceae species

Table 4. Cross-validation of discriminant functions for *A. albimanus* using five randomly selected data subsets

Subset no.	Derived from P/A[a]	Applied to P/A[a]	% Correctly predicted		Coefficients				Cut-off value
			As present	As absent	d_1	d_2	d_3	d_4	
1	18/19	9/27	89	81	0.526	−0.008	3.789	2.578	17.57
2	16/21	11/25	45	92	0.946	−0.008	4.624	6.208	32.61
3	9/28	18/18	72	94	0.263	−0.005	5.904	7.262	10.68
4	13/24	14/22	64	91	0.297	−0.005	3.994	3.947	11.08
5	11/26	16/20	69	95	−0.121	−0.003	7.007	3.400	−2.24
The whole data set			74	91	0.387	−0.006	4.428	4.306	13.68

General form of equation: $Z = d_1(T) + d_2(Alt) + d_3\arcsin(SB)^{1/2} + d_4\arcsin(BG)^{1/2}$, where T, temperature (°C); Alt, altitude (m); SB, submersed macrophytes (cover percentage after angular transformation); BG, cyanobacterial mats (cover percentage after angular transformation).

[a] P, number of sites with species present; A, number of sites with species absent.

Table 5. Cross-validation of discriminant functions for *A. crucians* using five randomly selected data subsets

Subset no.	Derived from P/A[a]	Applied to P/A[a]	% Correctly predicted		Coefficients				Cut-off value
			As present	As absent	d_1	d_2	d_3	d_4	
1	6/31	4/32	50	84	0.028	5.409	24.154	8.004	5.80
2	6/31	4/32	50	91	0.043	3.663	15.128	18.039	6.92
3	6/31	4/32	75	91	0.006	4.846	11.347	4.852	3.74
4	5/32	5/31	100	91	0.014	3.111	5.527	7.613	2.93
5	4/33	6/30	33	93	0.002	4.207	13.738	21.631	6.24
The whole data set			80	94	0.034	4.785	13.429	9.712	5.20

General form of equation: $Z = d_1(HA) + d_2\arcsin(EM)^{1/2} + d_3\arcsin(PER)^{1/2} + d_4\arcsin(DET)^{1/2}$, where HA, habitat area (m^2); EM, emergent macrophytes (cover percentage after angular transformation); PER, periphyton (cover percentage after angular transformation); DET, detritus (cover percentage after angular transformation).

[a] A, number of sites with the species absent; P, number of sites with the species present.

were present in Belize, but they did not support comparably high densities of *A. albimanus* larvae as in Mexico.

The DF for *A. crucians* was about as accurate as the DF for *A. albimanus*. Similarities in predictive accuracy of DFs for the two species reflect the tolerance of both species to a wide variety of habitats.

The fourth *Anopheles* included in the analysis, *A. argyritarsis*, was strictly associated with higher altitudes. Although this species was collected only at higher elevations, other collection records reveal that populations of *A. argyritarsis* also occur at lower elevations in KARST (Bertram 1971; unpublished observation). Therefore, any final conclusions about the association of this species with higher altitudes must await additional data.

Habitat Types. A second approach to larval analysis was based on the classification of habitats into habitat types according to their dominant vegetation. With 12 habitat types derived from 73 sampling sites, there were not enough replicates of each habitat type for detailed statistical analysis. However, using a *G* test of independence, several significant associations were found between mosquito larvae and habitat types. We were also able to rank the habitat types into groups of high, medium, and low densities of larvae. In our previous article (Rejmankova et al. 1992), we pointed out that, in addition to knowing whether habitats are associated with low, medium, or high larval densities, we also need to know the spatial and temporal extent of habitats to estimate their contribution to mosquito production. For example, habitat types of cyanobacterial mats and submersed–periphyton are in the high larvae-producing group in the dry season, whereas only cyanobacterial mats continue as high producers during the wet season. Evaluating the spatial distribution of individual habitat types in the regions should be a next step in our research effort.

Regions. Certain habitat types are related to specific regions, and they reflect the regional geology, hydrology, water, and soil quality. The MPR provides only two habitat types related to fast-flowing rivers and streams; i.e., rock pools and filamentous algae. The filamentous algae habitat type was not found very frequently in this region, probably because of a very low nutrient content of water. It is highly probable, however, that if streams and rivers from MPR became polluted, they would support more vigorous growth of filamentous algae and would provide a suitable habitat for *A. pseudopunctipennis* larvae. KARST is more diverse than MPR, but the most common habitat type (particularly in the dry season) was filamentous algae with associated populations of *A. pseudopunctipennis*. Populations of *A. albimanus* and *A. crucians* were found rather infrequently in KARST. Diverse fresh and

Table 6. Cross-validation of discriminant functions for *A. pseudopunctipennis* using five randomly selected data subsets

Subset no.	Derived from P/A[a]	Applied to P/A[a]	% Correctly predicted		Coefficients			Cut-off value
			As present	As absent	d_1	d_2	d_3	
1	8/29	6/30	100	100	0.004	−0.025	5.61	2.21
2	6/31	8/28	86	87	0.004	−0.092	24.50	7.73
3	5/32	9/27	78	93	0.005	−0.005	14.29	6.44
4	9/28	5/31	80	94	0.009	−0.120	11.28	3.37
5	7/30	7/29	100	90	0.010	−0.017	8.82	4.33
The whole data set			93	93	0.008	−0.050	12.32	4.79

General form of equation: $Z = d_1(Alt) - d_2(WD) + d_3\arcsin(FA)^{1/2}$, where Alt, altitude (m); WD, water depth (cm); FA, filamentous algae (cover percentage after angular transformation).

[a] P, number of sites with species present; A, number of sites with species absent.

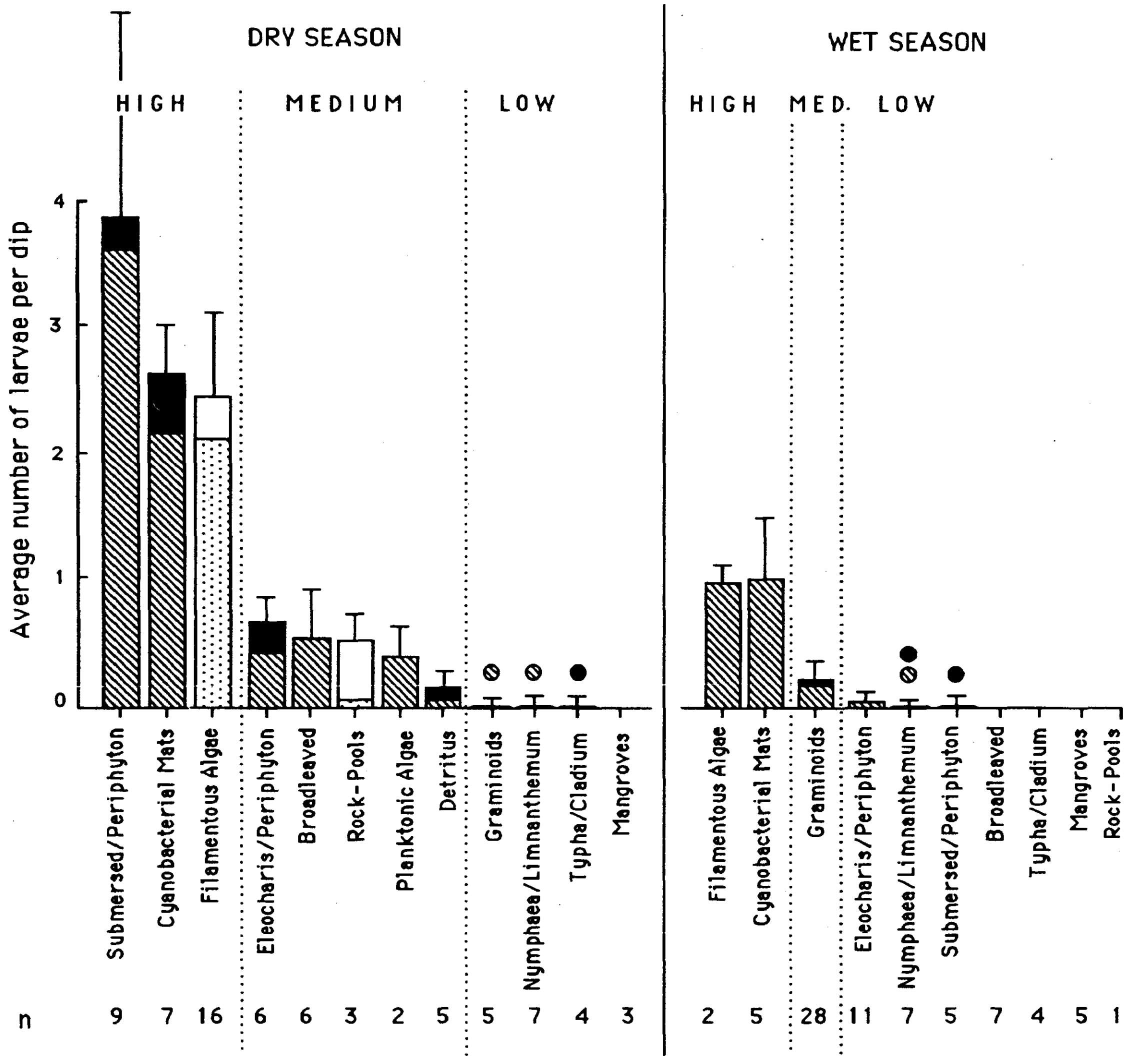

Fig. 3. Distribution of *Anopheles* species expressed as the average number of larvae per dip in individual habitat types. For the habitat description, see text. The number of sampling sites (*n*) belonging to each habitat type is indicated under the figure. Vertical bars indicate the standard error of mean. Wet season, September 1990; dry season, April 1991. For species description, see Fig. 5.

brackish water habitat types supporting both *A. albimanus* and *A. crucians* populations were encountered in CP. The habitat type cyanobacterial mats, which supports *A. albimanus*, was more frequent in CP (brackish). Habitat-types *Eleocharis*–periphyton and submersed–periphyton were common in CP (fresh).

During the wet season, neither *A. argyritarsis* nor *A. pseudopunctipennis* were found, most probably because their habitats were constantly flushed by heavy rains. This was similar to earlier findings in southern Mexico (Savage et al. 1990). Permanent bodies of water generally had the same habitat type and the same *Anopheles* species in both seasons. Larval densities were generally higher during the dry season than during the wet season; these differences may be related to smaller volumes of water being available in the dry season.

It is interesting that no environmental factors related to water chemistry, such as individual cation or anion concentrations, total suspended solids, or particulate organic matter, were found to be significantly correlated with the occurrence of larvae, except for *A. albimanus* in the wet season. Of all the environmental factors considered, dominant plant growth forms such as filamentous algae, cyanobacterial mats, submersed macrophytes, etc., showed the closest association with the larvae of particular *Anopheles* species.

Table 7. Transition of habitat-types from wet to dry season

Habitat type[a]	Sampled in wet season Total	Transition period from wet to dry season		Sampled in dry season		
		Dried	Contained water	Extant	Added	Total
BG	5	0	5	4	3	7
N–L	7	3	4	3	4	7
S–P	5	3	2	4	5	9
E–P	11	7	4	3	3	6
Br	7	5	2	0	6	6
Gr	28	23	5	4	1	5
T–C	4	4	0	2	2	4
FA	2	2	0	2	14	16
Ma	5	3	2	2	1	3
RP	1	0	1	1	2	3
De	0	0	0	0	5	5
PA	0	0	0	0	2	2

Numbers of habitats belonging to individual habitat types sampled in the wet season, dried out during the transition from the wet to dry season, containing water even in the dry season, added in the dry season, and total sampled in the dry season. Change from one habitat type to another during the transition period is indicated by arrows.

[a] BG, cyanobacterial mats; N–L, *Nymphaea–Limnanthemum;* S–P, submersed macrophytes–periphyton; E–P, *Eleocharis interstincta*–periphyton; Br, broadleaved; Gr, graminoids; T–C, *Typha–Cladium;* FA, filamentous algae; Ma, mangroves; RP, rock pools; De, detritus; PA, planktonic algae.

Physical factors (e.g., water depth, water temperature, and oxygen content) were usually marginally correlated with larval occurrence. This makes results of the analyses based on individual environmental factors very similar to those based on habitat types because the habitat types were defined by dominant plant forms.

The data presented here will eventually be used to develop a geographic information system on the distribution of malaria vectors in northern Belize. The analyses have led to additional questions related to malaria vector ecology: How soon do *A. argyritarsis* and *A. pseudopunctipennis* habitats develop in the dry season? How will the changes in land use (establishment of citrus plantations, increases in human population and migration, etc.) affect distribution and density of mosquito larval populations?

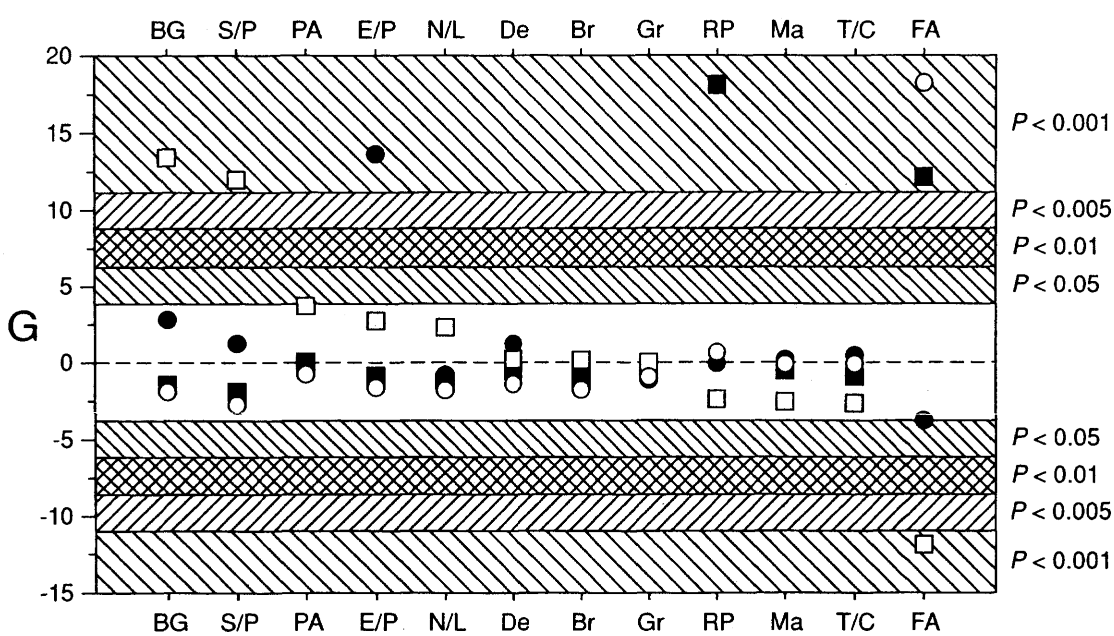

Fig. 4. *G* test of independence between the habitat-types and *Anopheles* larvae present (Belize, April 1991). BG, Cyanobacterial mats; S–P, submersed macrophytes–periphyton; PA, planktonic algae; E–P, *Eleocharis interstincta*–periphyton; N–L, *Nymphaea–Limnanthemum;* De, detritus; Br, broadleaved; Gr, graminoids; RP, rock pools; Ma, mangroves; T–C, *Typha–Cladium;* FA, filamentous algae. Empty square, *A. albimanus;* black square, *A. argyritarsis;* black circle, *A. crucians;* empty circle, *A. pseudopunctipennis.*

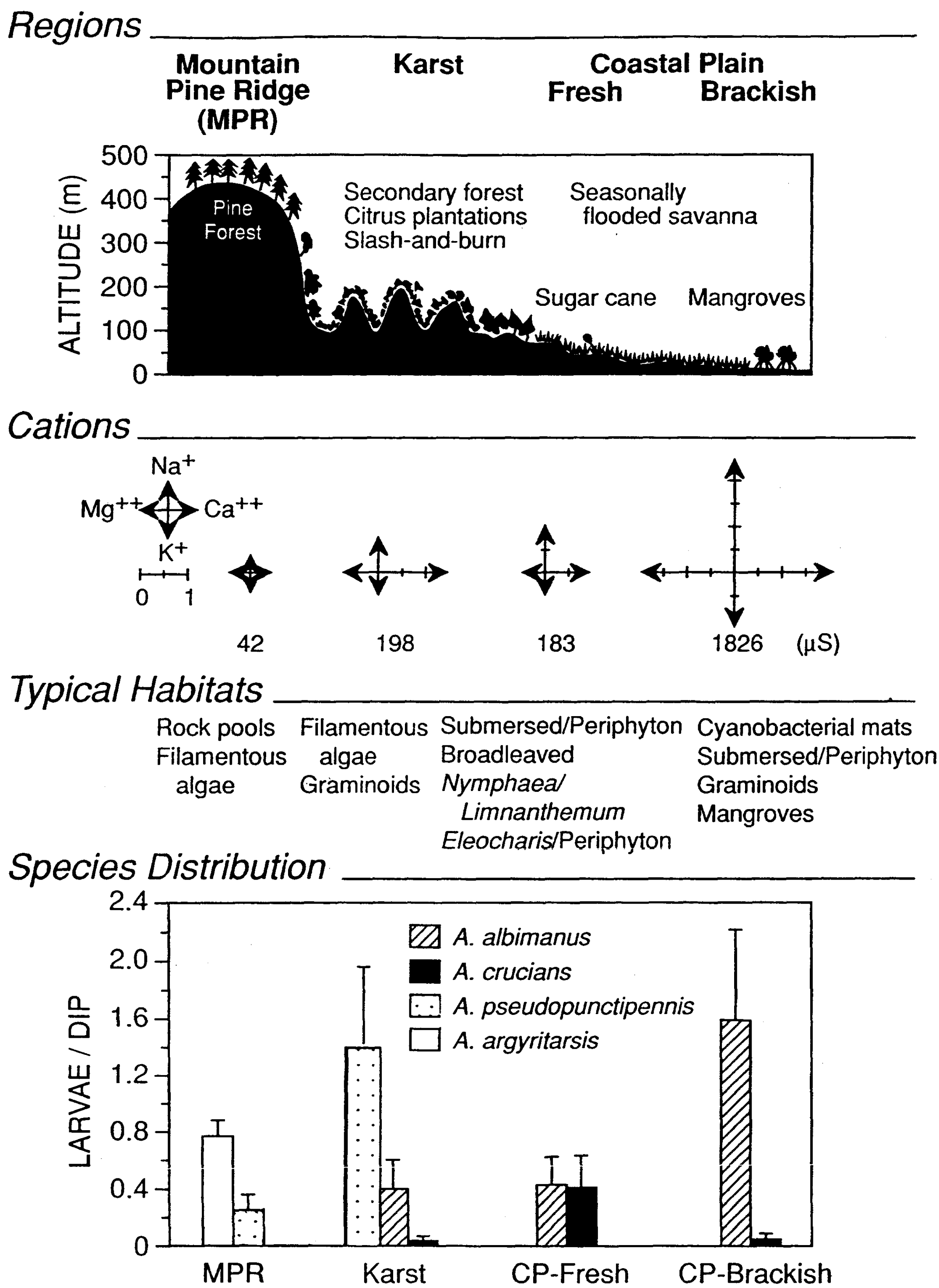

Fig. 5. Mosquito distribution according to physiographic region. Cation concentration is expressed in log mg/liter; numbers below cation diagrams express the specific conductivity. Larval densities for individual species are expressed as the mean number per dip per region; vertical bars indicate the standard error of the mean.

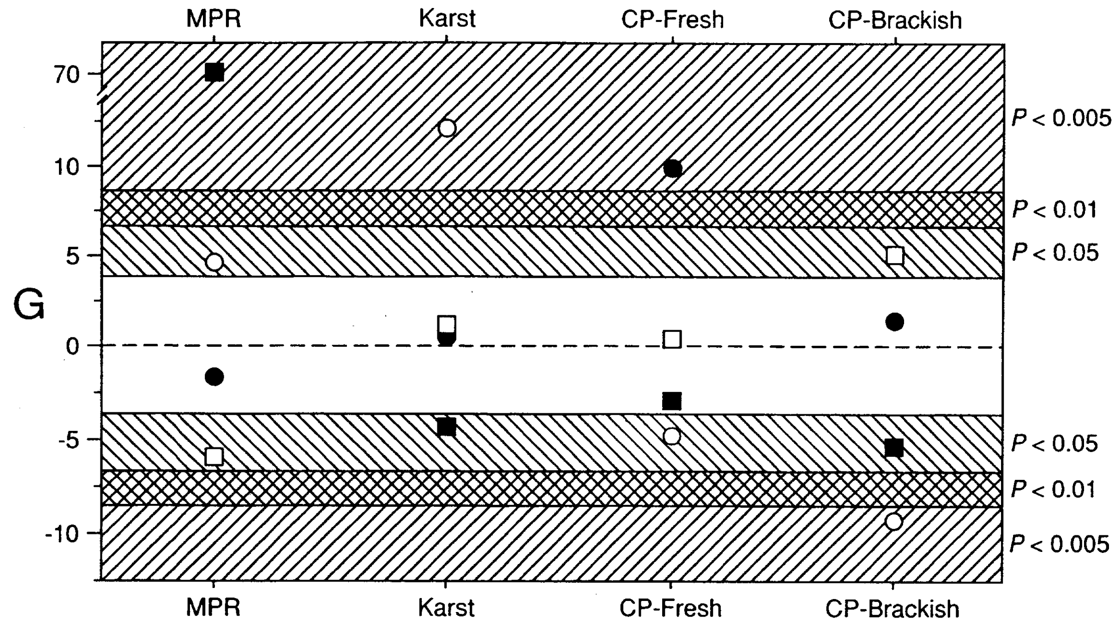

Fig. 6. *G* test of independence between the regions and presence of *Anopheles* larvae (Belize, April 1991). MPR, Mountain Pine Ridge; Karst, Karst and foothill region; CP (fresh), coastal plain, fresh water; CP (brackish), coastal plain, brackish water. Empty square, *A. albimanus;* black square, *A. argyritarsis;* black circle, *A. crucians;* empty circle, *A. pseudopunctipennis.*

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Appendix 1. List of plant species related to *Anopheles* spp. larval habitats; Belize, wet season, September 1990; dry season, April 1991

	Season[a] Wet	Dry
Emergent		
Gramineae		
Cynodon dactylon	+++	++
Distichlis spicata	++	–
Gramineae sp.	+++	++
Hymenachne amplexicaulis	++	–
Leptochloa sp.	++	–
Panicum sp.	++	–
Paspalum sp.	+++	+
Paspalum virgatum	++	–
Cyperaceae		
Cladium jamaicense	++	++
Cyperus articulatus	+	+
Cyperus ligularis	+	–
Cyperus odoratus	++	–
Cyperus peruvianum	+	+
Cyperus rotundus	++	–
Eleocharis caribea	++	–
Eleocharis cellulosa	++	–
Eleocharis intersticta	+++	+++
Eleocharis mutata	+	–
Eleocharis sp.	++	+
Fimbristylis spadicea	++	+
Fuirena umbellata	++	+
Rhynchospora barbata	++	–
Rhynchospora cephalotes	+	–
Rhynchospora cyperacea	++	–
Rhynchospora robusta	++	+
Rhynchospora setacea	+	–
Scleria pterata	++	–
Typha domingensis Typhaceae	++	++

Appendix 1. Continued

	Season[a] Wet	Dry
Broadleaved		
Bacopa monnieri	++	++
Batis maritima	+	–
Echinodorus sp.	++	+
Heteranthera sp.	–	++
Hydrocotyle sp.	+	–
Hymenocalis sp.	++	++
Justicia sp.	++	+
Lippia nodosa	+	+
Ludwigia octovalvis	+++	++
Pontederia sagittata	++	–
Polygonum sp.	++	++
Sagittaria lancifolia	+	–
Spilanthes sp.	++	++
Wedelia sp.	++	–
Rhizophora mangle	++	++
Floating		
Lemna sp.	+	–
Limnanthemum humbolti	++	++
Nymphaea ampla	++	++
Pistia stratiotes	–	+
Algae		
Filamentous	++	+++
Cyanobacterial mats	++	+++
Periphytic	++	+++
Submersed		
Cabomba sp.	–	++
Chara sp.	++	++
Mayaca fluitans	+	–
Naias guadalupensis	++	+
Potamogeton sp.	–	++
Utricularia cornuta	+	–
Utricularia foliosa	++	++
Utricularia resupinata	++	++
Utricularia purpurea	++	++

[a] +++, species occurring frequently; ++, species occurring less frequently; +, species occurring infrequently; –, species not found.

Appendix 2. Detailed Description of Habitat Types

Emergent

Graminoids. Prevalent in the wet season in marshes and seasonally flooded wetlands such as edges of pools and lagoons. Average height above the water surface is 30 cm; often grows to 60 cm; usually not very dense, average cover is 30%. Typical for CP and KARST; fresh waters.

***Eleocharis interstincta*–Periphyton.** A common habitat type in the wet season, present in most depressions in seasonally flooded savanna, usually forming large uniform areas with plants up to 40 cm tall and covering ≈50% of the water. *Utricularia foliosa* as a submersed codominant is quite frequent. This habitat type is less common during the dry season as many habitats become dry. Those dry season habitats with water have senescent *Eleocharis* which is often covered with dense periphyton (Cyanobacteria and Chlorophyta). Typical for CP with fresh or sometimes slightly brackish waters.

***Typha–Cladium*.** Represented by very tall (up to 3 m) and usually very dense (90% cover) emergent macrophytes, mostly *Typha domingensis* or *Cladium jamaicense;* occurring in relatively permanent marshes in both wet and dry seasons and in both fresh and slightly brackish waters.

Broadleaved. Very broad and diverse group of habitats, often containing *Ludwigia octovalvis* as a dominant species. Sometimes low shrubs are present. This, often species-rich, habitat type is generally found on edges of ponds, ditches, and pools and is typical for seasonally flooded areas where aquatic vegetation does not have time to develop. This habitat type is absent in the dry season.

Mangroves. Mostly *Rhizophora mangle* with no other vegetation occurring in salt or brackish waters. This habitat type is present in both wet and dry seasons.

Floating

***Nymphaea–Limnanthemum*.** Floating-leaved macrophytes in more or less permanent fresh waters of ponds and lagoons. Often relatively dense, large, rigid leaves cover the water surface.

Cyanobacterial Mats. Large dense floating mats (scums) consisting of microscopic benthic Cyanobacteria, known also as blue–green algae (e.g., *Phormidium, Lyngbya*). The mats usually develop on the bottom of a water body, then gradually rise to the water surface. Where present, they usually cover large areas. A special microclimate develops in these mats with very pronounced diurnal fluctuations of O_2, pH, and temperature. More frequent in the dry season but also present in the wet season.

Submersed

Submersed Macrophytes–Periphyton. Several species of submersed macrophytes, such as *Mayaca fluitans, Naias guadalupensis, Potamogeton lucens, Chara* spp., often forming dense populations which may break the water surface. This habitat type develops in mostly permanent water bodies, even though some can grow in seasonally flooded roadside ditches and temporary pools. In the dry season, submersed macrophytes are often densely overgrown with periphytic algae.

Filamentous Algae. Predominantly *Spirogyra* species typical of small rock pools in river beds in both MPR and rivers of KARST. Present mainly in the dry season. During the wet season, this habitat type does not have time to develop because river pools are constantly flushed by heavy rains.

Planktonic Algae. Eutrophic water such as cattle ponds; not common and not sampled in the wet season.

Without Vegetation

Rock Pools, No Filamentous Algae. A temporary habitat type present in the dry season in MPR.

Detritus. This habitat type usually develops in small water bodies with fallen leaves and other plant debris.